

Table 2. Global comparisons of reproductive characteristics in scleractinian corals from the Caribbean, Red Sea, and Pacific regions. See individual entries under regional headings for literature citations

	Caribbean	Hawaii	Central	Pacific GBR	Okinawa	Red Sea
No. of species for which reproductive data are recorded	19	17	47	145	26	15
Gonochoric	6	4	4	34	2	0
Hermaphroditic	10	6	28	109	24	15
Not reported	3	7	15	2	0	0
Brood	12	5	14	8	1	3
Spawn	7	9	28	136	25	11
Not reported	0	3	5	1	0	1
No. of species in region	62 <sup>1</sup>	45 <sup>2</sup>	353 <sup>3</sup>	356 <sup>4</sup>	242 <sup>5</sup>	244 <sup>6</sup>

Sources: (1) Goreau & Wells (1967), (2) Jokiel (1987), (3) R. Randall, pers. comm., (4) Willis et al. (1985), (5) Veron (1985), (6) Sheppard (1987)

Table 3. Summary of reproductive mode for 210 species of scleractinian corals for which data are available. Entries reflect cumulative counts, omitting repeats for species found in 2 or more regions

	Hermaphroditic	Gonochoric	Unknown
Spawn	131	37	0
Brood	11	7	19
Unknown	1	2	390+

She also noted that Caribbean *Porites*, which are brooders, have small adult colony size, while the spawning gonochoric Pacific *Porites* are large and long-lived. Pacific *Porites* species which brood form small, encrusting colonies (*P. stephensoni* [as *P. haddoni*], Marshall & Stephenson 1933; *P. murrayensis*, Kojis & Quinn 1981 b; *P. brighami*, Hunter & Hodgson unpubl.).

#### Timing, seasonality, synchrony, and periodicity

Sexual reproduction in corals may occur yearly (Willis et al. 1985, Babcock et al. 1986), seasonally (Rinkevich & Loya 1979a, b, Szmant 1986, Tomascik & Sander 1987), monthly (Marshall & Stephenson 1933, Kawaguti 1941, Atoda 1947 a, Richmond & Jokiel 1984), or not at all (Grigg et al. 1981, Richmond 1985, Richmond & Hunter unpubl.). Annual multispecies synchronous spawning has been observed for over 140 species on the Great Barrier Reef (Harrison et al. 1984, Willis et al. 1985, Babcock et al. 1986, Harrison pers. comm.), while asynchrony is exhibited among coral species in the Central Pacific, Hawaii, Okinawa, and the Red Sea (Table 1). Synchronous development and release of gametes among individuals in a population

are important to maximize the probability of successful cross (and/or self) fertilization. Conversely, a presumed advantage to multiple spawnings or planulations is to minimize the effects of a single catastrophic event on an individual's or population's reproductive success.

Temperature, photoperiod, and nocturnal illumination all appear to be important in providing temporal cues which may allow synchrony within populations (Kojis & Quinn 1981 a, Jokiel et al. 1985, Willis et al. 1985, Hunter 1989). The expanding database suggests that the degree of multispecies synchrony may be correlated with the annual temperature range experienced by the corals (Shlesinger & Loya 1985, Babcock et al. 1986). Annual variation in seawater temperature is 2.2 °C in the Central Pacific (Guam; Emery 1962), 3.2 °C in the Caribbean (Barbados; Tomascik & Sander 1987), 4.0 °C in Hawaii (Oahu; Jokiel 1985), 6.0 °C in the Red Sea (Eilat; Rinkevich & Loya 1979 b), 9.8 °C in Okinawa (Nakamura 1984), and 12.0 °C on the Great Barrier Reef (Magnetic Island; Babcock et al. 1986). The percentage of reported coral species spawning within the same month and lunar phase for each of these regions is 18, 26, 29, 20, 65, and 88 %, respectively. Oliver et al. (1989) reported that reproductive seasonality and synchrony among and within coral species distributed from the southern Great Barrier Reef to Papua New Guinea diminishes at lower latitudes. The trend appears to be one of tighter interspecific synchrony with increased temperature range. A similar pattern of less restricted spawning patterns with increasing proximity to the equator was reported for echinoderm species by Pearse (1968).

Differences in reproductive seasonality can occur within a species over its distributional range (Table 4). Most Great Barrier reef species spawn in the austral spring, while spawnings in the Central Pacific, Hawaii,



Table 4. Global comparisons of reproductive periodicity in coral species which have been reported from 2 or more regions. Abbreviations are for month and lunar day. Month is divided into 8 phases: 1, new moon, 3, first quarter, 5, full moon, 7, last quarter; 2, 4, 6 and 8 indicate intermediate lunar phases (after Shlesinger & Loya 1985); w: winter, sp: spring, sr: summer, f: fall, yr: year-round; \* possibly sterile

	GBR	Central Pacific	Okinawa	Hawaii	Red Sea
<b>ACROPORIDAE</b>					
<i>Acropora cerealis</i>	Nov, 6	Jul, 4-5	-	-	-
(as <i>A. hystrix</i> ) <sup>a</sup>		sr			
<i>Acropora cytherea</i>	Oct/Nov, 6	-	Jun, 5	*	-
(as <i>A. corymbosa</i> ) <sup>b</sup>		Jun/Jul, 1-4			
<i>Acropora digitifera</i>	Oct, 6	Jun, 5			
<i>Acropora florida</i>	Nov, 6	-	Jun, 5?8	-	-
<i>Acropora formosa</i>	Oct, 6/Nov, 5-6	-	Jun, 5?8	-	-
<i>Acropora grandis</i>	Nov, 6	-	Jun, 5	-	-
<i>Acropora humilis</i>	Oct, 6/Nov, 5-7 (spawn)	Jun/Jul, 1-3 (brood) Aug, 7 (spawn)	-	*	May/Jul, 7 (spawn)
<i>Acropora hyacinthus</i>	Oct/Nov, 5-6	-	Jun, 5	-	Jul, 3
(as <i>A. surculosa</i> ) <sup>c</sup>		Jul, 7-8			
<i>Acropora latistella</i>	Sep/Oct, 6	-	Jun, 7	-	-
<i>Acropora loripes</i>	Nov/Dec, 6				
(as <i>A. squarrosa</i> ) <sup>d</sup>		Jul, 2-3			
<i>Acropora microphthalmia</i>	Oct/Nov, 6	-	Jun, 5/7	-	-
<i>Acropora nasuta</i>	Nov, 6-7	Jul, 7-8 Aug, 6-7	-	-	-
<i>Acropora nobilis</i>	Oct/Nov, 6		Jun, 5		
<i>Acropora robusta</i>	Nov, 6				
(as <i>A. smithi</i> ) <sup>e</sup>		Jul, 4-5			
<i>Acropora selago</i>	Nov, 6	*			
(as <i>A. delicatula</i> ) <sup>f</sup>					
<i>Acropora tenuis</i>	Oct, 6	Jul, 6	Jun, 5	-	-
	Nov, 5-6				
<i>Acropora valida</i>	Oct, 6-7	Jul, 7-8	Jun, 5	*	-
	Nov, 5-6				
(as <i>A. variabilis</i> ) <sup>g</sup>	sp-sr	sr			
<i>Montipora aequituberculata</i>	Oct, 6	-	Jun, 5-6	-	-
<i>Montipora digitata</i>	Oct/Nov, 5	-	Jun, 5-6	-	-
<i>Montipora turgescens</i>	Nov, 6	-	Jun, 5	-	-
<b>FAVIIDAE</b>					
<i>Favia fava</i>	Nov, 6	-	-	-	Jun/Jul, 6-7 Aug, 6
<i>Favia mathaii</i>	Nov, 5-6	Jul, 7-8	-	-	-
<i>Favia pallida</i>	Oct/Nov, 6	-	Jun, 5	-	-
<i>Favia stelligera</i>	Nov, 6	Jul, 7-8	-	-	-
<i>Favites abdita</i>	Nov, 5-6	sr	-	-	-
<i>Favites chinensis</i>	Nov, 6	-	Jun, 6-7/Jul, 7 Aug, 7	-	-
<i>Favites flexuosa</i>	Nov, 6	sr	-	-	-
<i>Goniastrea aspera</i>	Oct, 5-7	Oct/Nov, 1 (broods?)	Jun/Jul, 5-6	-	-
	Nov, 5-6 (spawns)				
<i>Goniastrea edwardsi</i>	Nov, 6	sr	-	-	-
<i>Goniastrea retiformis</i>	Nov, 6	Jul, 1-2	-	-	Jul/Aug, 7
<i>Leptoria phrygia</i>	Nov, 6	Jul, 7-8	-	-	-

<sup>a</sup> Synonymized with *A. cerealis* by Veron & Wallace (1984)

<sup>b</sup> Synonymized with *A. cytherea* by Veron & Wallace (1984)

<sup>c</sup> Synonymized with *A. hyacinthus* by Veron & Wallace (1984)

<sup>d</sup> Synonymized with *A. loripes* by Veron & Wallace (1984)

<sup>e</sup> Synonymized with *A. robusta* by Veron & Wallace (1984)

<sup>f</sup> Synonymized with *A. selago* by Veron & Wallace (1984)

<sup>g</sup> Synonymized with *A. valida* by Veron & Wallace (1984)



Table 4 (continued)

	GBR	Central Pacific	Okinawa	Hawaii	Red Sea
<b>FAVIIDAE</b>					
<i>Montastrea curta</i>	Nov, 6	Aug, 6-7	-	-	-
<i>Platygyra daedalea</i>	Oct/Nov, 6-7	Jul, 6-7	-	-	-
<i>Platygyra lamellina</i>	Nov, 6-7	-	-	-	Jun/Jul, 1-2 Aug, 1
<i>Platygyra pini</i>	Nov, 6	sr	Jun, 2	-	-
<b>FUNGIIDAE</b>					
<i>Fungia fungites</i>	Oct/Nov, 6	sr	-	-	-
<i>Heliofungia actiniformis</i>	Oct/Nov, 5	Sep-Apr, 1	-	-	-
<b>MUSSIDAE</b>					
<i>Lobophyllia corymbosa</i>	Nov, 6	-	Jun, 6	-	-
<i>Symphyllia recta</i>	Nov, 6	-	Jun, 5	-	-
<b>OCULINIDAE</b>					
<i>Galaxea fascicularis</i>	Oct/Nov, 6 (spawns)	Jul, 2-3 (spawns) yr (broods)	Jun/Jul/Aug, 6-7 (spawns)	-	Jul/Aug/Sep, 6-7 (spawns)
<b>POCILLOPORIDAE</b>					
<i>Pocillopora damicornis</i>	yr, 1-5	yr, 1 yr, 3-8 Jun/Jul, 1-4	-	yr, 5-3	-
<i>Pocillopora verrucosa</i>	-	Jan, 1-4 (broods)	-	-	Jul/Aug, 1 (spawns)
<i>Seriatopora hystrix</i>	sp-sr	sr/w, 1-8	-	-	-
<i>Stylophora pistillata</i>	-	yr, 5-7	-	-	Dec-Jul, 1-8
<b>PORITIDAE</b>					
<i>Porites cylindrica</i>	Nov, 6	*	-	-	-
<i>Porites lobata</i>	Nov, 6	Jul, 7-8	-	Aug, 7-8	-
<i>Porites lutea</i>	Dec, 1, 4-7, 8 Jan, 4-8 Nov-Jan Nov, 5-7	sr	-	-	-

Okinawa, and the Red Sea occur mostly during summer. For many species, variations in timing and synchrony of spawning have been observed within as well as between the regions summarized in this paper (Table 1). Seasonal (latitudinal) variability within regions (e.g. between Palau, Enewetak and Guam) may be of sufficient magnitude to cause differences in reproductive timing. In addition, spawning may occur at different times for different sections of a single colony, or for different colonies within a population (Willis et al. 1985, Babcock et al. 1986, Hunter & Richmond unpubl.).

While temperature may be the seasonal cue, nocturnal illumination (lunar phase) may provide the 'fine tuning' for the particular night or nights of gamete or planula release. Both brooding and broadcasting species have been shown to cue on night-time illumination (Jokiel et al. 1985, Hunter 1989). It has also been suggested that tidal regime and onset to darkness may play roles as 'forcing functions', determining the actual time of day when spawning will occur (Harriott 1983 a, Babcock et al. 1986, Hunter 1989).

A distinct lunar planulation cycle was reported for *Stylophora pistillata* in Palau (Atoda 1947 b), while Red Sea populations of this species show no lunar synchrony (Rinkevich & Loya 1979 b). Lunar periodicity of planulation was found to differ between populations of *Pocillopora damicornis* at Enewetak and Hawaii, and within populations in Hawaii (Richmond & Jokiel 1984). The 'Type B' morph of *P. damicornis* planulated consistently at first quarter moon, while 'Type Y' planulated at last quarter. Van Moorsel (1983) proposed identification of a new species of *Agaricia* based partly on its distinct planulation schedule.

Differences in timing among allopatric populations of a species may represent adaptations to local environmental parameters and cues. Richmond & Jokiel (1984) suggested that asynchrony among sympatric populations of an identified 'species' may be the result of the immigration of planulae from one region into another. Reproductive isolation, in this case via temporal mechanisms, allows for divergence and eventual speciation. Such reproductive differences within nominal



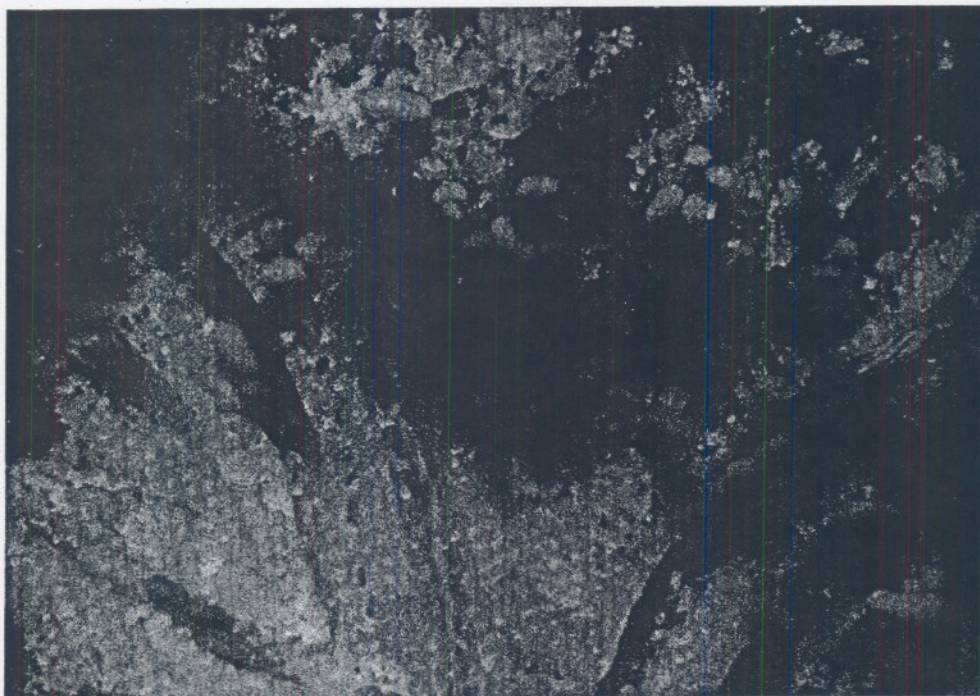


Fig. 1. *Acropora tenuis*. Section through a ripe colony of a simultaneous hermaphrodite, 1 wk prior to spawning. Egg and sperm are found within the same polyp. Egg diameter is ca 0.5 mm

species raise questions concerning taxonomy based on morphological characteristics alone.

#### Asexual reproduction in corals

Corals possess the ability to reproduce asexually, which is displayed by a variety of mechanisms. Asexual reproductive processes include formation of 'polyp-balls' (Rosen & Taylor 1969), polyp bail-out (Goreau & Goreau 1959, Sammarco 1982, Richmond 1985), asexual production of planulae (Stoddart 1983), and fragmentation (Highsmith 1982).

Asexual reproduction via fragmentation appears to be important for many coral species, and especially for populations living at the extremes of their physiological limits. Grigg et al. (1981) reported lack of mature gonads in populations of 3 species of *Acropora* from the Northwest Hawaiian Islands. Reproduction via fragmentation appeared to be the major means of population growth. Likewise, *Pocillopora damicornis* populations in the eastern Pacific had not produced mature gonads nor planulae during a 2 yr study, yet were the dominant reef species off the coast of Panama (Richmond 1985). Eastern Pacific *P. damicornis* exhibit higher colony growth rates than Central Pacific populations, which enhances population growth via fragmentation (Richmond 1985). High bioerosion rates on corals in the eastern Pacific are proposed as making fragmen-

tation important for massive species such as *Pavona cactus* (Highsmith 1982).

Asexual reproduction of corals is found in all regions covered in this review, but appears to dominate in areas which are marginal for coral growth, including the eastern Pacific (Richmond 1985), the northwest Hawaiian Islands (Grigg et al. 1981), southwestern Australia (Stoddart 1984), and possibly Bermuda (Wyers 1985). Within regions with optimal conditions for coral growth, asexual processes may dominate specific habitats including areas of high wave energy (Tunncliffe 1981), soft or unconsolidated substrata (Gilmore & Hall 1976), and stable, undisturbed sites (Hunter 1988, unpubl.). In areas where sexual reproductive processes are prevalent, asexual reproduction may augment recruitment at any time, especially during periods of environmental stress or disturbance (Highsmith et al. 1980).

Enhanced colony growth rate and subsequent fragmentation may result from allocation of energy away from production of sexual products, notably in environments where sexual processes may be physiologically constrained (Richmond 1987a). The occurrence of sterile populations has been described for other invertebrate taxa as well (Mileikovsky 1971). Asexual reproduction has the advantages of not requiring a partner, propagating locally adapted genotypes, and providing a refuge-in-size from predation and burial by sediments.



### PLANULA LARVAE

Coral planulae can result from either internal fertilization and brooding, or external fertilization of spawned gametes and subsequent development outside the parent colony (Harrigan 1972, Babcock & Heyward 1986). Stoddart (1983) suggested that planulae of *Pocillopora damicornis* may also be produced asexually, based on similarities of parental and planular multilocus genotypes and adult population structure. Two other species, *Tubastrea coccinea* and *T. diaphana*, were also found to have planulae with isozyme patterns identical to their broodparents, while planulae of *Acropora palifera* and *Seriatopora hystrix* had genotypes consistent with sexual origin (Ayre & Resing 1986).

The brooded planulae of *Pocillopora damicornis* contain symbiotic zooxanthellae upon release from the parent, as well as a large quantity of lipid (Fig. 2). With the additional ability to feed while planktonic, these planulae remain competent for over 100 d, a period sufficient to allow dispersal over large distances (Richmond 1981, 1987 a). Planulae resulting from spawned gametes (Fig. 3) may lack zooxanthellae upon fertilization (known exceptions being poritids and *Montipora* spp., whose eggs contain maternal zooxanthellae), but eventually acquire the algal cells from the environment, usually after settlement and metamorphosis (Babcock 1989). Planulae of *Fungia scutaria* acquire zooxanthellae after release from the parent colony but before metamorphosis (Krupp 1983).

The spawned larvae of *Acropora tenuis* do not contain zooxanthellae, and have a shorter competency period (ca 20 d) than the brooded larvae of *Pocillopora*

*damicornis* (Richmond 1989). Larval competency (the ability of larvae to successfully settle and metamorphose) is a major factor affecting the distribution of coral species, particularly for reefs in the eastern Pacific. It has been proposed that the present coral fauna of the eastern Pacific is the result of long-distance dispersal of planulae from Central Pacific stock (Dana 1975, Richmond 1987 b). Some instances of limited distribution patterns and endemism may be the result of abbreviated larval competency periods.

### RECRUITMENT

Reproductive success may best be measured by recruitment. Recruitment of both sexual and asexual propagules is mediated by biotic factors, such as predation and competition, and by abiotic factors such as environmental variability and disturbance. Sexual recruitment of corals is a function of several parameters including the timing of reproduction, competency periods of planula larvae, current regimes, availability of substrata, and densities of predators and competitors (Birkeland et al. 1981, Fitzhardinge 1985, Babcock 1989). Several studies have found evidence for 'open populations' with non-localized sources of coral planulae (Wallace 1985 a, Babcock 1989), but others have suggested that reefs can be self-seeded (Baggett & Bright 1985, Sammarco & Andrews 1988, 1989, Andrews et al. 1989). In some areas, juvenile abundance is directly related to adult cover (Bak & Engel 1979,

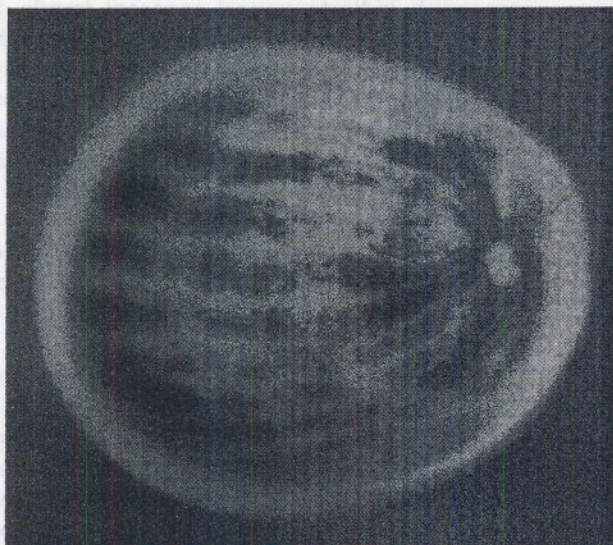


Fig. 2. *Pocillopora damicornis*. Brooded planula of a coral. Note the bands of zooxanthellae, and the oral opening. The larva is ca 1 mm in length

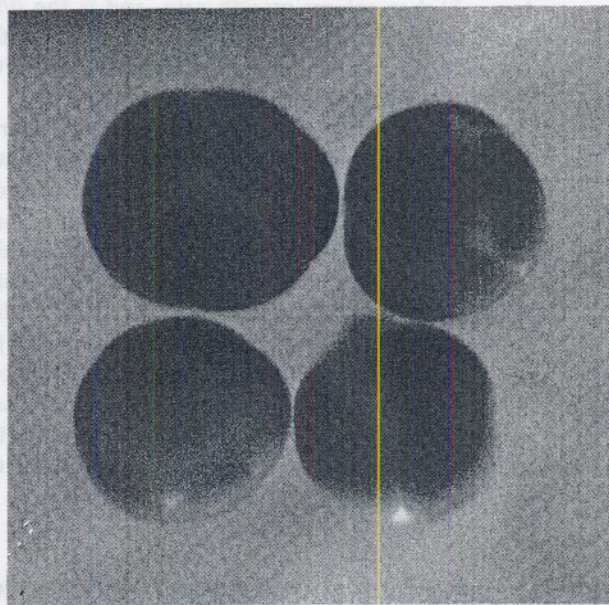


Fig. 3. *Acropora tenuis*. Spawned clusters of eggs surrounding sperm from a coral. Each cluster contains between 9 and 16 eggs around a single sperm packet. Cluster diameters range between 1.3 and 1.6 mm